

A new osmiine bee with a spectacular geographic disjunction: *Hoplitis (Hoplitis) onosmaevae* sp. nov. (Hymenoptera, Anthophila, Megachilidae)

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Abstract

A new osmiine bee species, *Hoplitis (Hoplitis) onosmaevae* sp. nov. (Megachilidae), is described. So far, this species is exclusively known from the Mercantour National Park in the southwestern French Alps and from mountainous ranges in Turkey and northern Iraq, two areas separated by at least 2000 km. Phylogenetic analyses based on mitochondrial and nuclear genes revealed that *H. onosmaevae* is closely related to *H. adunca* (Panzer, 1798), *H. benoisti* (Alfken, 1935) and *H. manicata* (Morice, 1901). *Hoplitis onosmaevae* is presumably narrowly oligolectic and harvests pollen only on flowers of *Onosma* L. (Boraginaceae). It has a particularly long proboscis, which is probably an adaptation to collect nectar from the long-tubed flowers of this plant genus. The females collect pollen by buzzing the *Onosma* flowers, a rare behavior in megachilid bees. The species nests in insect burrows in dead wood, similar to *H. adunca* and *H. manicata* but unlike other closely related representatives of the subgenus *Hoplitis*, suggesting a single origin of nesting in dead wood and hollow stems in this lineage. In France, *H. onosmaevae* inhabits alpine steppe-like habitats close to forests and appears to be extremely local, since only two populations are currently known. The conservation status of this extremely rare bee species in Europe is discussed.

Résumé

Une nouvelle espèce d'abeille appartenant à la tribu des Osmiini, *Hoplitis onosmaevae* sp. nov. (Megachilidae), est décrite. Elle est à ce jour connue du Parc national du Mercantour dans le Sud des Alpes françaises et de zones montagneuses de Turquie et du Nord de l'Irak, deux aires distantes de plus de 2000 km. Des analyses phylogénétiques de gènes mitochondriaux et nucléaires indiquent que cette nouvelle espèce est apparentée à *H. adunca* (Panzer, 1798), *H. benoisti* (Alfken, 1935) et *H. manicata* (Morice, 1901). *Hoplitis onosmaevae* est certainement oligolectique, spécialisée pour la récolte du pollen sur les fleurs d'*Onosma* L (Boraginaceae). Elle est caractérisée notamment par un proboscis très allongé, qui est probablement une adaptation à la collecte du nectar dans les fleurs de ce genre botanique. Les femelles en exploitent le pollen en les faisant vibrer («buzzing»), comportement rare au sein de la famille des Megachilidae. Il a été observé que cette nouvelle espèce nidifie dans des galeries existantes dans le bois mort, à l'instar de *H. adunca* et de *H. manicata*, mais contrairement à d'autres représentants du sous-genre *Hoplitis*, ce qui suggère une origine unique de l'emploi du bois mort et des tiges creuses en tant que substrat de nidification au sein de ce groupe. En France, *H. onosmaevae* semble extrêmement localisée : elle n'a été trouvée que sur deux stations, correspondant à des habitats d'altitude d'affinité steppique, non loin de boisements. Son statut de conservation en Europe est discuté.

Key Words

Anthophila, Apiformes, *Hoplitis*, *Onosma*, osmiine bees, buzzing, conservation, France, Iraq, Turkey

Introduction

Hoplitis Klug, 1807 is the most diverse genus of the bee tribe Osmiini (Megachilidae) with 389 described species, about 80% of which occur in the Palaearctic (Müller 2023a). Fourteen subgenera of *Hoplitis* are currently recognized (Praz et al. 2008; Sedivy et al. 2013c; Müller 2023a) and nearly 60% of the described species belong to *Hoplitis (Alcidamea)* Cresson, 1864, *Hoplitis (Anthocopa)* Lepeletier & Serville, 1825 and *Hoplitis (Hoplitis)* Klug, 1807. The nominal subgenus, which is restricted to the Palaearctic and whose type species is the widespread and common *H. adunca* (Panzer, 1798), is the largest, with 93 described species. The representatives of the subgenus *Hoplitis* can be classified into six species groups, of which four correspond to former subgenera (Michener 2007): the *adunca* (*Hoplitis* s. str.), the *annulata* (*Annosmia* Warncke, 1991), the *erythrogaster* (*Bytinskia* Mavromoustakis, 1954) and the *persica* (*Coloplitis* Griswold, 1998) groups. The two additional species groups are the *bassana* and the *monstrabilis* groups (Sedivy et al. 2013c). While several new *Hoplitis (Hoplitis)* species have recently been described from Europe and Morocco (Müller 2012, 2016, 2022), more than 50 species belonging to this subgenus, mainly from Turkey, the Levant and Central Asia, remain undescribed (Müller 2023b).

Species of the subgenus *Hoplitis* are mostly oligoleptic or mesoleptic and collect the pollen either only on Boraginaceae or Fabaceae or on both of them. The pattern of frequent transitions between the exploitation of these two plant families among related species and the frequent exploitation of both families by the same species has been referred to as the “Boraginaceae-Fabaceae paradox” (Sedivy et al. 2013a). Within the Boraginaceae, the genus *Echium* L. is exploited by many species, but some species also collect the pollen from other genera, such as *Onosma* L., *Lithodora* Grisebach or *Heliotropium* L. Numerous species have particular morphological adaptations for pollen collection, such as hooked bristles on the proboscis or on the fore legs (Müller 2012; Sedivy et al. 2013a). Regarding nesting biology, different behaviours are found within this subgenus. Probably all species of the *annulata* and *monstrabilis* groups nest in the ground in self-excavated burrows (Rozen et al. 2009; Sedivy et al. 2013b; Le Goff 2017; Fateryga et al. 2023; Müller 2023b). Most species of the *adunca* group build their nests exposed in shallow depressions of rocks and stones or hidden within rock cavities and use sand as nesting material, often combined with small pebbles and hardened with salivary secretions, e.g. *Hoplitis anthocopoides* (Schenck, 1853) or *H. loti* (Morawitz, 1867) (Sedivy et

al. 2013b). Two species of the *adunca* group nest in insect borings in dead wood or in hollow stems, in addition to other preexisting cavities, and use sand to separate their brood cells: *H. adunca* and *H. manicata* (Morice, 1901) (Müller 2023b; Sedivy et al. 2013b).

We describe here a new *Hoplitis* species of the *adunca* group. This new species was detected during faunistic inventories of the Mercantour National Park in the Alps in southern France. Upon morphological comparison, the French specimens were found to exactly correspond to specimens of an undescribed species from southern Turkey. In the present publication, this new species is morphologically diagnosed, its phylogenetic position within the subgenus *Hoplitis* is explored using genetic analyses, and its nesting biology and floral association are described based on field observations in southern France and microscopical analysis of pollen contained in the female scopae.

Material and methods

Abbreviations and symbols

FL1, FL2,...	flagellar segment 1, flagellar segment 2...
	(following scape and pedicel);
T1, T2,...	first metasomal tergum, second metasomal tergum...;
S1, S2,...	first metasomal sternum, second metasomal sternum...;
ETHZ	Eidgenössische Technische Hochschule Zürich, Entomological collection, Switzerland;
MAC	Private collection of Matthieu Aubert, Pégairolles-de-Buèges, France;
MNHN	Muséum national d'Histoire naturelle, Paris, France;
NMPC	National Museum (Natural History), Prague, Czech Republic;
OLML	Oberösterreichisches Landesmuseum, Linz, Austria.

Material studied

The following material was examined for this study: 1. males and females of the undescribed species from Mercantour National Park, France, from southern and eastern Turkey and northern Iraq; 2. males and females of *Hoplitis holmboei* (Mavromoustakis, 1948), *H. homalocera* Zanden, 1991, and *H. linguaria* (Morawitz, 1875),

which are Boraginaceae specialists and also possess a very long proboscis (Sedivy et al. 2013a), that served for comparison. As no specimens of a fourth *Hoplitis* species with an extraordinarily long proboscis, *H. semilinguaria* Tkalcú, 1992 (known only in the female sex), could be located neither in NMPC nor in OLML (Tkalcú collection), where the types should be deposited according to the original description, the comparison was performed based on the original description.

Terminology

Morphological and anatomical terminology is based on Michener (2007).

Equipment

Morphological examination of specimens was done with a Perfex Sc 6.38 binocular (7× to 45× magnification). Measurements were realized with a micrometric eyepiece. All pictures of collected and prepared specimens were taken with a Keyence VHX 1000 digital microscope. A reflex body Nikon D7200 combined with a macro lens Nikkor 60 mm were used for field photographs.

Geographical informations

French collecting sites were georeferenced using a field GPS. Turkish and Iraqi specimens were collected by different entomologists between 1968 and 2022 (see list of paratypes below and Suppl. material 1 for details) and the label information regarding the collecting sites is heterogeneous. In case the coordinates were not indicated on the label, they were extrapolated from the locality data. All coordinates are given in WGS 84. The distribution map was generated using QGIS Desktop 3.28.3 and AutoNavi Satellite layer.

Microscopical pollen analysis

Pollen was removed from the metasomal scopa of five females from France (one specimen) and three localities in Turkey (four specimens) as well as from two brood cells of a nest discovered in France, embedded in glycerol gelatine on a slide and compared with reference slides containing pollen of different Boraginaceae species and genera under a microscope at 400× magnification.

Genetic analyses

For two individuals of the new species collected in Saint-Dalmas-le-Selvage, France, in 2020 (see list of paratypes below), we sequenced four gene fragments included in

the phylogenetic study of Sedivy et al. (2013c): the mitochondrial gene *cytochrome oxidase I* (COI) and three nuclear genes *conserved ATPase domain* (CAD), *elongation factor 1-alpha* (EF) and *long-wavelength rhodopsin* (Opsin), using standard DNA sequencing protocols and primers developed for bees or for Megachilidae (Praz et al. 2008; Litman et al. 2011; Sedivy et al. 2013c). Genetic distances were computed using the Kimura 2-parameter (K2P) distance model in a test version of Paup 4.0 (Swofford 2002) kindly provided by D. Swofford. The new sequences have been deposited on Genbank (accession numbers PP389027–PP389032) and BOLD (accession numbers HYMAA896-24 and HYMAA897-24). Single gene analyses were performed using maximum Likelihood in RAxML 8.2 (Stamatakis 2014), using a single partition and a GTR + G model; the four genes were then concatenated and analysed using RAxML. We implemented two distinct partitioning schemes: first, with four partitions, one per gene; and second, with seven partitions, three for the three nucleotide positions of COI, three for the three nucleotide positions of the nuclear genes, and one partition for the introns; in both cases, a GTR + G model was fitted to each partition.

Results

Field work during summer 2018 in the Mercantour National Park on flowers of *Onosma tricerosperma* subsp. *fastigiata* (Braun-Blanq.) G. López, 1994 (Boraginaceae) by the first author led to the capture of several *Hoplitis* specimens of the *adunca* species group, which were characterized by an extraordinarily long proboscis, a feature not known from other French or Central European species. Upon closer examination, these specimens were found to belong to an undescribed species, which was already known from southern Turkey. Other *Hoplitis* species with a very long proboscis, such as *H. holmboei* from Cyprus, *H. homalocera* from the Levant and *H. linguaria* from eastern Turkey and the Caucasus, differed morphologically, as did *H. semilinguaria* from Iran based on the original description.

Genetic analyses

The two COI sequences obtained for the two French individuals of the new species were identical to each other. Queries carried out with the identification tool of the BOLD systems (www.boldsystems.org) suggested that the closest relatives are *Hoplitis adunca* (89.86–90.48% identity), *H. benoisti* (Alfken, 1935) (89.35–89.71%) and *H. manicata* (85.68–86.42%). Based on COI, the genetic distances between the new species and *H. adunca*, *H. benoisti* and *H. manicata* were 10.98%, 11.05% and 14.9%, respectively.

Phylogenetic analyses of the concatenated, four-genes dataset placed the new species in a strongly supported clade (Bootstrap support, hereafter BS, 100%) that also included *H. adunca*, *H. benoisti* and *H. manicata* (Fig. 1).

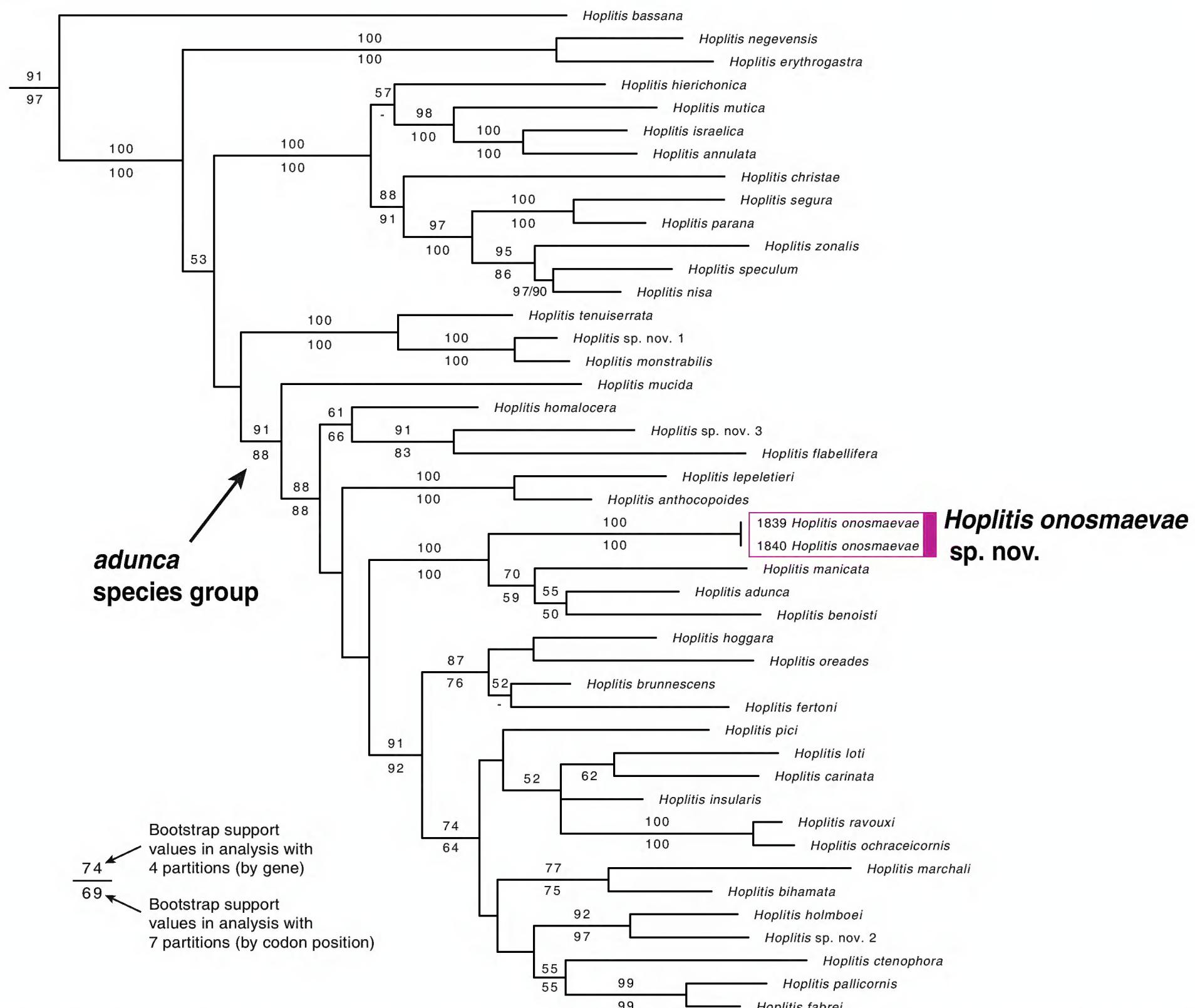


Figure 1. Phylogenetic tree based on maximum likelihood analyses of sequence data of the mitochondrial gene COI and of the three nuclear genes conserved ATPase domain (CAD), elongation factor 1-alpha (EF) and long-wavelength rhodopsin (Opsin). Numbers above branches: statistical support based on 1000 bootstrap replicates (values below 50 are omitted) in the analysis with 4 partitions (by gene); number below branches: support in analysis with 7 partitions (by codon position; a hyphen under a node indicates that this node was not recovered in the analysis); the topology is from the analysis with 4 partitions.

Within this clade, the new species was sister to these three species, although this relationship was only very weakly supported (BS 59–70%). The new species, which is characterized by a particularly long proboscis (see below), was not closely related to two other long-tongued species, *H. holmboei* and *H. homalocera*; there was no genetic data available for *H. linguaria* and *H. semilinguaria*.

Taxonomy

Hoplitis (Hoplitis) onosmaevae Aubert, sp. nov.

<https://zoobank.org/9DAA5D35-8EC4-441F-8180-0A063BFBD30F>

Figs 3–14, 16–21, 24

Type material. **Holotype.** FRANCE • ♀; Alpes-Maritimes, Tinée Valley, Saint-Etienne-de-Tinée, across from

Bousiéyas, southern slopes of L'Alpe Mountain (type locality part of Mercantour National Park); 44.315°N, 6.859°E; 1985 m; 13.7.2018; Matthieu Aubert leg.; *Onosma* stand; MNHN (inventory number: EY35781).

Paratypes. FRANCE (2♀, 3♂) • 1♀, 1♂; same data as for holotype; ETHZ (♀) and MNHN (♂) coll. (MNHN inventory number: EY35831) • 1♂; Alpes-Maritimes, Tinée Valley, Saint-Etienne-de-Tinée, across from Bousiéyas, southern slopes of L'Alpe Mountain; 44.319°N, 6.858°E; 1920 m; 13.7.2018; Matthieu Aubert leg.; *Onosma* stand; ETHZ. • 1♀, 1♂; Alpes-Maritimes, Tinée Valley, Saint-Dalmas-le-Selvage, vallon du torrent de Jalorgues, Boudin/Bouding; 44.272°N, 6.843°E; 1705 m; 23.6.2020; Matthieu Aubert leg.; MAC. IRAQ (1♂) • 1♂; Dahuk governorate, Mt. Gara; 37.015833°N, 43.350556°E; 1912 m, 11.5.2023, D. Baiocchi leg.; D. Baiocchi coll. TURKEY (4♀, 6♂) • 1♂; Bolu province, Bolu lake env.; 21.6.1993;

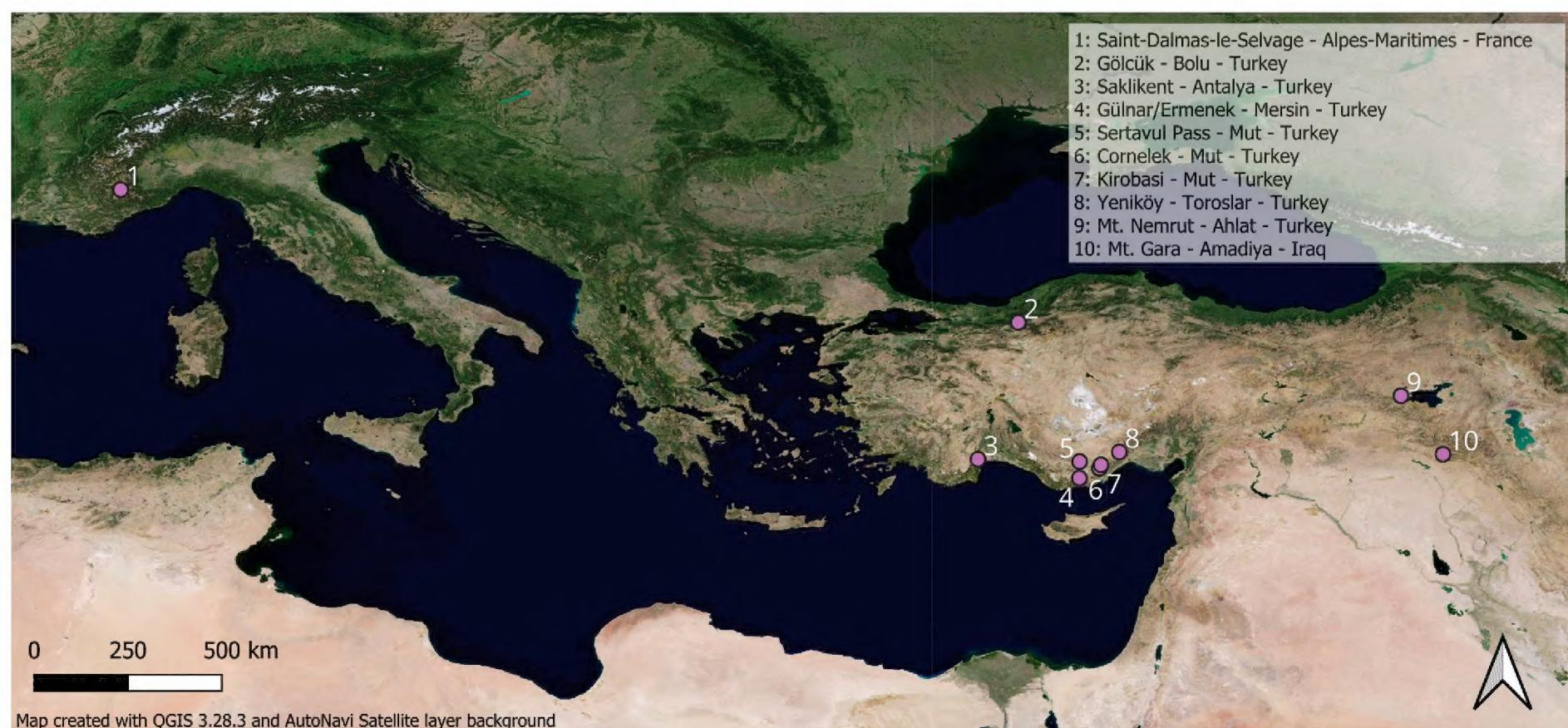


Figure 2. Distribution map of *Hoplitis onosmaevae* sp. nov.

M. Halada leg.; ETHZ. • 2♂; Antalya province, 4 km east of Saklikent; 36°52.51'N, 30°30.954'E; approx. 1600 m; 30.5.2009; John S. Ascher, Jerome G. Rozen, Hikmet Özbebek leg.; ETHZ. • 1♀; Mersin province, Mersin district, between Gülnar and Ermenek; 36°21.380'N, 33°18.841'E; 1075 m; 24.5.2006; Erwin Scheuchl leg.; ETHZ. • 1♀; Mersin province, Mut district, Sertavul Pass; 36.812°N, 33.32°E; 1300 m; 7.6.1968; Josef Gusenleitner leg.; ETHZ. • 1♀; Mersin province, Mut district, Kirobasi; approx. 36.723°N, 33.900°E; 1450 m; 19.6.1997; Marek Halada leg.; ETHZ. • 1♀; Mersin province, Mut district, 40 km east of Cornelek; approx. 36.630°N, 33.866°E; 1700 m; 29.5.1996; Mi. Halada leg.; ETHZ. • 1♂; Mersin province, Toroslar district, Yeniköy; 37.08°N, 34.41°E; 1200 m; 29.5.1993; Stephan Risch leg.; ETHZ. • 2♂; Bitlis province, Mount Nemrut, 36.626°N, 42.186°E; 2350 m; 25.5.1989; Klaus Warncke leg.; ETHZ.

See Suppl. material 1 for a complete list of records as well as Fig. 2 for a distribution map.

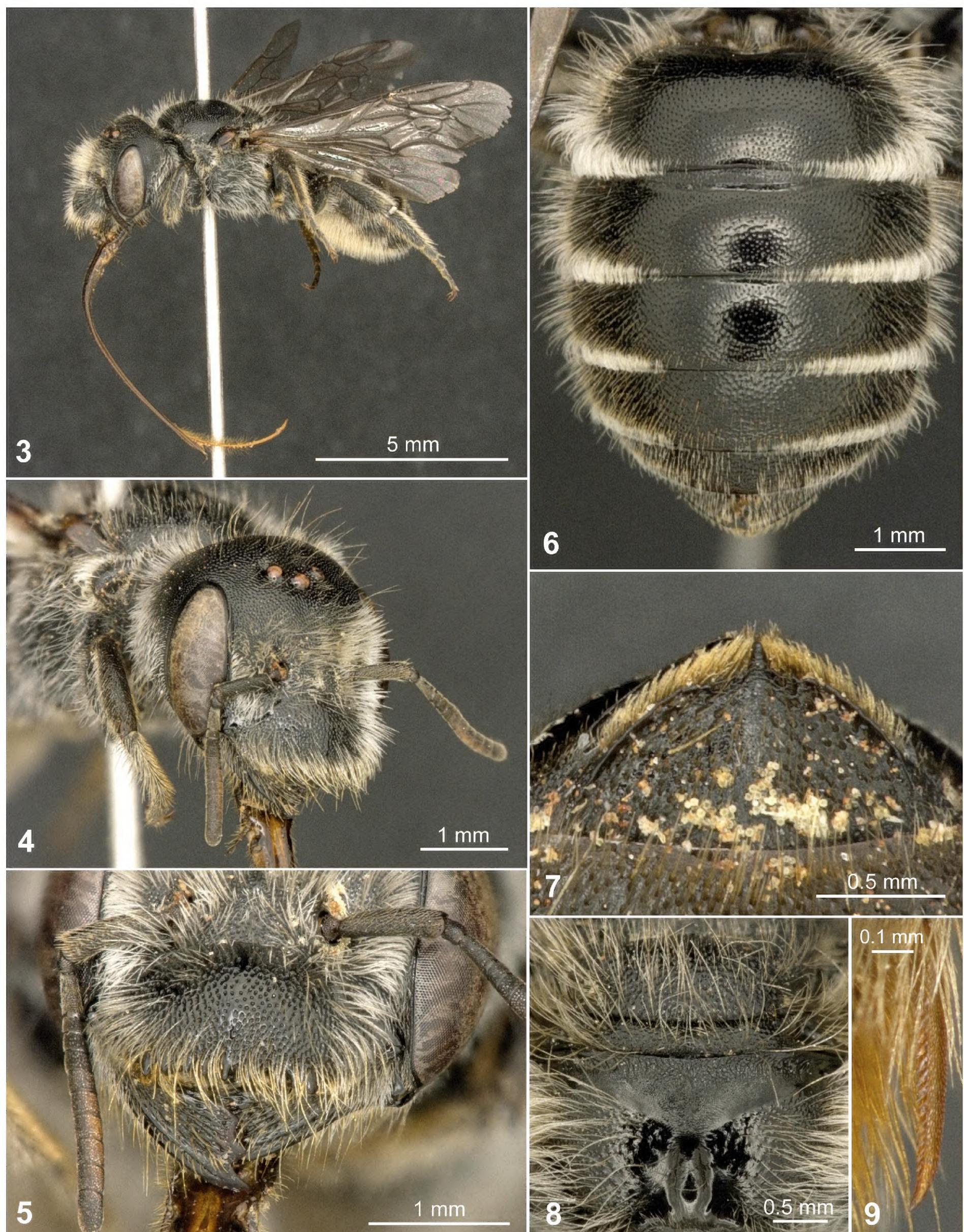
Diagnosis. In most species of *Hoplitis* (*Hoplitis*), the length of the proboscis is at most one-third as long as the body. Only *H. linguaria*, *H. holmboei*, *H. homalocera* and *H. semilinguaria* have a longer proboscis, which reaches about half of the body length. *Hoplitis onosmaevae* possesses an even longer proboscis, which is approximately as long as the body (Fig. 3). In both sexes of *H. holmboei* and *H. homalocera*, the vertex is comparatively short (ocelloccipital distance less than two ocellar diameters) and, when seen in front view, not elevated behind ocelli, but regularly rounded across its width; in *H. onosmaevae* the vertex is longer (ocelloccipital distance about three ocellar diameters) and is strongly elevated behind ocelli (Figs 3, 4). *Hoplitis onosmaevae* differs from *H. linguaria* in both sexes by the color of the tegulae, which are reddish-orange in *H. linguaria* and brown (although often reddish brown along the external margin) in *H. onosmaevae*. In the female, *H. onosmaevae*

can be distinguished from *H. linguaria* by the lateral margins of S6, which have a thickened rim, and by the apical margin of S6, which ends medially in a sharp spine as in *H. adunca* (Fig. 7); in *H. linguaria*, S6 lacks thickened rims or a medioapical spine. Moreover, the punctuation of the supraclypeal area in *H. onosmaevae* is comparatively fine and dense with only small interspaces especially in the middle, whereas it is sparse in *H. linguaria* in the middle. In the male, *H. onosmaevae* can be distinguished from *H. linguaria* by the shape of the membranous appendage at the apical margin of S6 and the form of the gonostylus. In *H. onosmaevae*, the appendage of S6 is longitudinally raised medially, wider at the base than at the apex, tapers into a narrowed tip and is covered with short light orange hairs in the middle (Figs 12, 14). The gonostylus is threadlike and slightly clubbed at the apex. In *H. linguaria*, the membranous appendage of S6 is flat, short and distinctly bilobed and the gonostylus is much thicker and narrowed at the apex. Compared to *H. semilinguaria*, which is known only in the female, the inner margins of the compound eyes are diverging towards the clypeus in *H. onosmaevae*, whereas they are parallel in *H. semilinguaria*. In addition, S6 of *H. linguaria* lacks thickened marginal rims as is probably also the case in *H. semilinguaria*. Tkalcu (1992) compared these two species and did not provide any information on the structure of S6.

Hoplitis onosmaevae can be separated from the common species *H. adunca*, which is similar in size and also has thickened marginal rims and a medioapical spine on female S6, by the yellowish-brown hind tibial spurs (Fig. 9) (tibial spur black in *H. adunca*), in addition to the longer proboscis.

Description. Female (habitus: Figs 3, 18–20, 24). Body length 9–10 mm.

Integument color. Cuticula generally black, except where indicated hereafter. Proboscis brown, glossa or-



Figures 3–9. *Hoplitis onosmaevae* sp. nov., female (holotype). **3.** Lateral view; **4.** Head; **5.** Clypeus and mandibles; **6.** Metasoma, dorsal view; **7.** Last sternum, ventral view; **8.** Propodeum; **9.** Inner spur of hind tibia, posterior view.

ange. Cuticula reddish-brown laterally along apical margin of clypeus and more or less along margin of sternites and tergites, on internal surface of femora, apical part of leg segments, especially last tarsi and claws. All

tibial spurs yellowish-brown to orange. Tegulae dark brown, external margin often reddish brown. Wing venation dark brown. Eyes grey-brown in the field. **Vestiture color.** Generally white, including scopa, except where in-

dicated hereafter. Hairs slightly darker, greyish brown, on scutum. Some hairs along apical margin of clypeus and on tergal discs yellowish white. Hairs on internal surface of tibiae and tarsi, on basal part of femora and apical half of trochanters yellowish-orange.

Head. Vertex strongly elevated and tilted forward when seen in front or 3/4 view. Ocellooccipital distance approximately equal to three ocellar diameters (Fig. 4). Inner margin of compound eyes slightly diverging below (ratio between upper and lower interocular distance approximately 0,92). Clypeus strongly convex, protruding, apical margin with approximately nine teeth, lateral teeth triangular, median teeth nearly cylindrical (Figs 4, 5). Mandibles tridentate, apical tooth elongate, acute (Fig. 5). Proboscis equal to body length when fully extended, galea half as long as body, with short bristles basally. Labrum longer than wide. Head overall shiny, shagreened only on parts of clypeus (see below), densely punctate; interspaces absent or narrow, except on vertex and genae where interspaces can be as wide as one puncture diameter, on frons laterally and close to ocellar area where the interspaces can reach two puncture diameters. Frons along frontal line and supraclypeal area more densely and finely punctate (supraclypeal area sometimes comprises some narrow interspaces centrally). Clypeus more strongly punctate than elsewhere on head, interspacers up to 1 or 2 puncture diameters, punctuation becoming denser and finer apically; clypeus in basal half with median impunctate longitudinal line (Fig. 5), line sometimes reaching apical margin. Labrum unpunctured and shiny in basal third, mat and shagreened apically, here more or less punctate. Proboscis surface unpunctured, smooth and shiny on the front, mat and shagreened laterally and dorsally. **Antennae.** FL2 slightly longer than FL3 and FL4 together; FL (5–6)–7–10 brown-orange below (Fig. 5).

Mesosoma. Pronotum weakly shagreened with shallow punctuation, but shiny. Mesepisternum (except ventral part), scutum and scutellum shiny, densely and relatively strongly punctate, interspaces well visible, up to 2 to 3 puncture diameters on central part of scutum. Mesepisternal concavity shiny with sparse punctuation. Axillae shagreened, densely and finely punctate. Metanotum shiny with distinct punctuation. Metepisternum weakly shagreened but shiny. Propodeal triangle nearly entirely shagreened, shiny in its lower part; propodeal posteriorly nearly impunctate around propodeal pit, more densely punctate laterally; sides of propodeum densely and finely punctate (Fig. 8). Mesepisternum ventrally impressed along longitudinal axis, this concavity open posteriorly between mid-legs insertions, here shiny and sparsely punctate. Mesosoma entirely hairy except on propodeal triangle and propodeal pit (Fig. 8). Hairs on scutellum, lateral part of mesepisternum and on propodeum as long as on vertex, shorter on scutum and even more so on ventral parts of mesepisternum. **Legs.** External extensions on apex of first and mid tibiae relatively thin, elongated and curved. Spur of front tibiae modified, internal margin lamellar, external margin thick and curved, apex of spur

pointed, internally with a minute fringe of hairs. Front metatarsi basally with an internal notch. Inner spurs of hind tibiae straight and regularly tapering, only slightly curved apically (Fig. 9).

Metasoma. T1 smooth and shiny, unpunctured on vertical part, disk with regular, sparse punctuation (interspacers up to 4 puncture diameters), punctuation denser and finer toward the margin. T2–3 similar to T1, but impressed basally, punctuation sparser on T2 than on T1, becoming even sparser on T3. T4 similar to T3, slightly more shagreened, punctuation rugose. T5–6 shagreened, punctuation denser and more rugose than on T4. All terga with a thin impunctate margin, impunctate margin larger on T6. In fresh specimens, T1–4 laterally with long erect white hairs, hairs on T1 as long as those on scutellum; T1–4 with white, interrupted apical fasciae, T5 with continuous apical fasciae, T6 with decumbent, light hairs. S1–6 shiny but slightly shagreened with moderately dense (2 to 3 puncture diameters), rugose punctuation, their margin impunctate. S6 laterally with a thickened rim, rim interrupted before apex; apex pointed (Fig. 7).

Male (habitus: Figs 16, 17). Body length 10–12 mm.

Integument color. As in ♀ except when mentioned below. Eyes grey-green in the field. **Vestiture color.** Predominantly brown-orange in fresh specimens, fading to yellowish to greyish white.

Head. Vertex as in ♀. Inner orbital edges slightly diverging below (less so than in ♀). Clypeus protruding, apical margin denticulate, but less regularly and strongly than in ♀; teeth partly hidden by dense apical fringe of hairs. Mandibles bidentate, upper tooth short, apical tooth sharp. Proboscis, galea and labrum proportions as in ♀. Vestiture very dense on frons, paraocular and supraclypeal areas and clypeus. Punctuation overall more homogeneous than in ♀, finer and denser on average; clypeus entirely punctate except a narrow impunctate area along lateral margins, punctuation fine and dense, difficult to see due to dense vestiture. Labrum medially shiny, unpunctured or with sparse punctuation, shagreened and more densely punctate laterally. **Antennae.** Scape densely punctate and hairy, 3 times as long as wide at apex; width at apex twice basal width. FL2 triangular, at most 1,5 as long as wide at apex, as long as FL3 and FL4 together. FL3 and FL4 twice as wide as long. FL8–10 nearly square, FL11 approximately 1,5 times as long as wide. Flagella flattened dorso-ventrally; only internal surface of FL2 (distinctly) and FL3 (slightly) convex. FL5– or FL6–11 orange ventrally (Figs 10, 11).

Mesosoma and legs. As in ♀ except where indicated hereafter. Punctuation denser and finer on scutum and lateral parts of mesepisternum, and denser on area around propodeal pit.

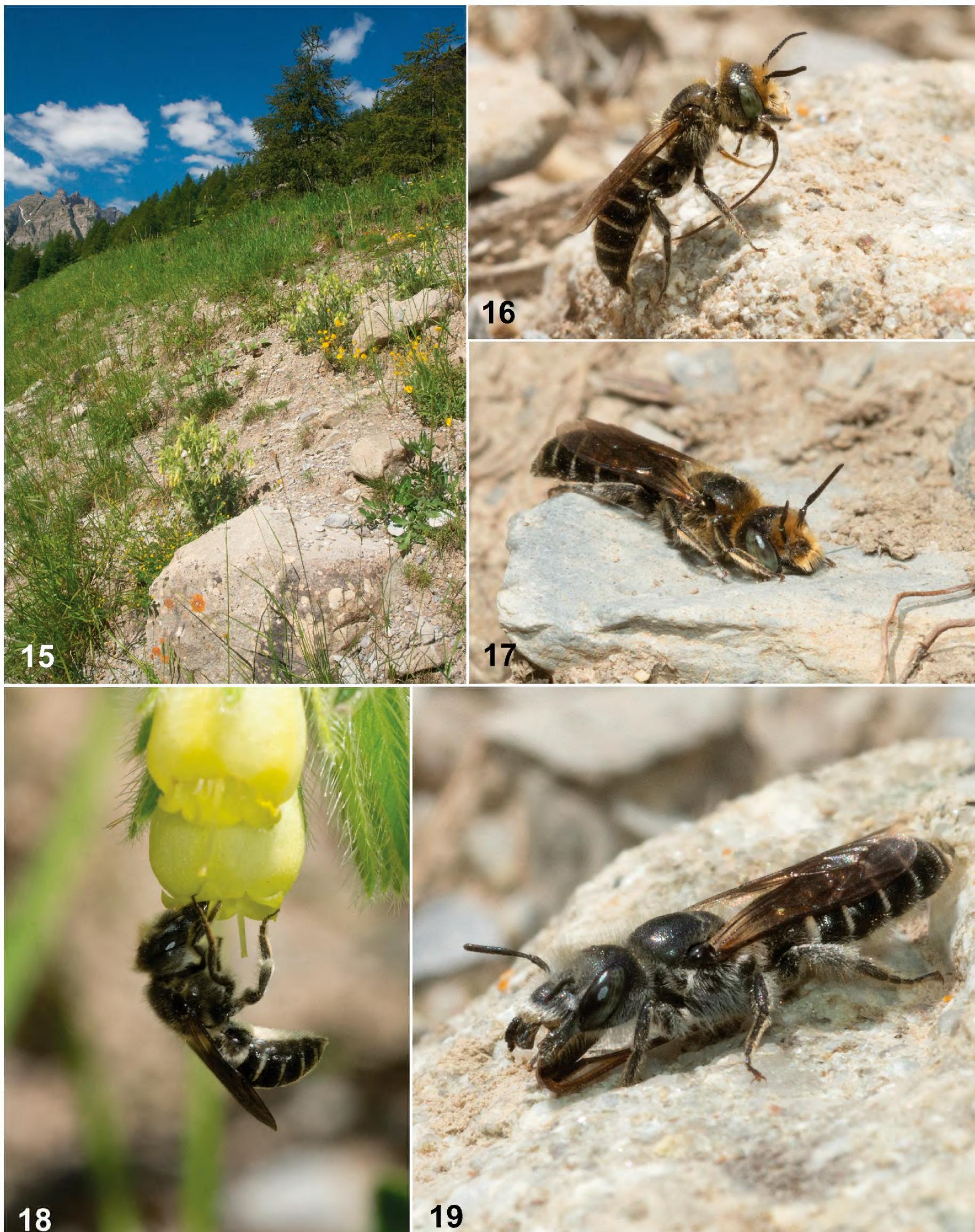
Metasoma. Tergal punctuation generally as in ♀ but punctures less impressed and area with fine punctuation on tergal margins wider. T7 finely punctate and shagreened basally, smooth and shiny medially, punctuation becoming rugose and sparse apically. T2–3 depressed basally. T6 with a strong tooth laterally, apical margin irregular, slightly sinuate medially. In dorsal view, lateral margin of



Figures 10–14. *Hoplitis onosmaevae* sp. nov., male. **10.** Left antenna, dorsal view; **11.** Left antenna, front view; **12.** Sterna 3–6 (the metasoma was slightly extended to expose S6); **13.** Terga 5–7, dorsal view; **14.** Membrane appendage of sternum 6, lateral view.

T7 slightly concave medially, apical margin rounded (Fig. 13). Metasomal vestiture as in ♀ except where indicated hereafter. Lateral fasciae of T1 less pronounced and more elongated, T2–5 with shorter hairs, T6 with continuous fasciae on apical margin, fasciae narrower in the middle but not interrupted, T7 with long hairs laterally but fewer hairs medially. S1 thicker than S2–4, with lamellar margin. S2–5 with a transverse premarginal gibbosity (inconspicuous on S5), S5 with longitudinal central groove. Margins of S1–4 slightly sinuate, S5 straight medially, rounded laterally. S6 basally with short and wide translucent lamella, median extension trapezoidal, with sinuate

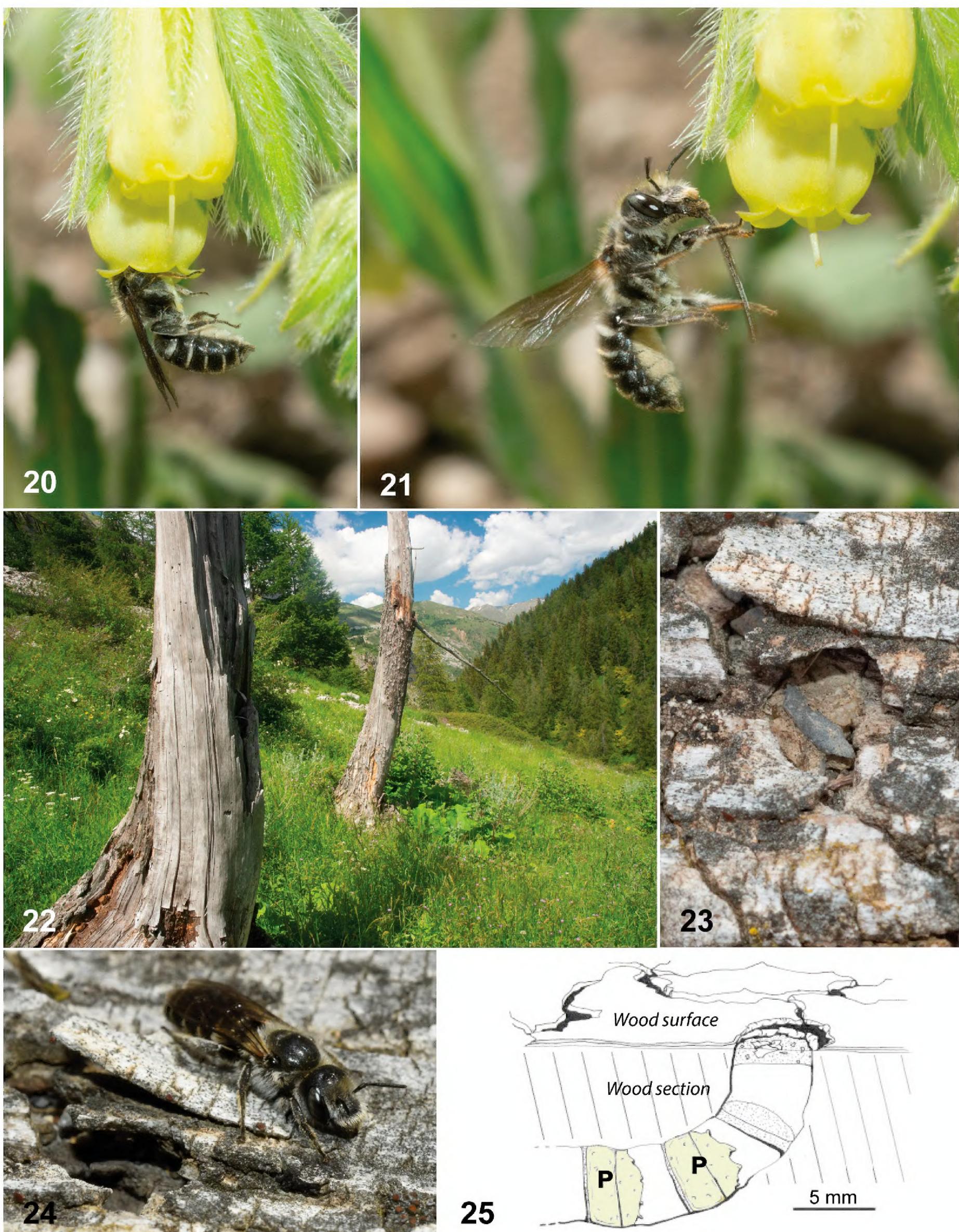
margins (Figs 12, 14; see also Diagnosis). S1 with strong and dense punctuation on thickened part. S2–4 with dense punctuation, shagreened and with fine punctuation basally and premarginally, transverse gibbosities smooth and shiny, with sparse punctuation medially. Median extension of S6 mostly shagreened (Fig. 14). Apical margin of S1–3 with sparse fringe of relatively long hairs, apical fringe shorter on S4, almost absent on S5. S6 baso-laterally with dense and long fringe of hairs, hairs emerging behind translucent lamella; surface of median extension of S6 with short yellowish-orange hairs. Gonostyli thread-like, slightly clubbed apically.



Figures 15–19. *Hoplitis onosmaevae* sp. nov., foraging habitat and behaviour (France, Saint-Dalmas-le-Selvage, 23.6.2020). **15.** Foraging habitat with patch of the host plant, *Onosma tricerosperma* subsp. *fastigiata*; **16.** Male resting on stone between two patrolling flights, with unfolded proboscis; **17.** Male resting on stone between two patrolling flights; **18.** Female on a flower of *Onosma tricerosperma* subsp. *fastigiata*; **19.** Female concentrating nectar with widely open mandibles.

Etymology. The species epithet *onosmaevae* refers to the assumed close association with plants of the genus *Onosma* (see section on pollen hosts below) and to Maëva Gardenat, to whom the first author wishes to dedicate this species.

Distribution. Known so far from the Mount Gara in northern Iraq (Dahuk Governorate), from the Nemrut Dağ in Eastern Turkey (Bitlis province), from the western and central Taurus Mountains in southern Turkey



Figures 20–25. *Hoplitis onosmaevae* sp. nov., nesting habitat and behaviour (France, Saint-Dalmas-le-Selvage, 23.6.2020, for photographs). **20.** Female in buzzing position on a flower of *Onosma tricerosperma* subsp. *fastigiata*; **21.** Female leaving a flower of *Onosma tricerosperma* subsp. *fastigiata*; **22.** Nesting habitat with dead trunks of larch; **23.** Nest entrance plugged with sand and pebbles; **24.** Female near the nest entrance, which is visible at the bottom left; **25.** Cross-section of nest (P = pollen provisions).

(Antalya and Mersin province), from the western Pontic Mountains in northwestern Turkey (Bolu Province) and from the Tinée Valley in the French southern Alps

(Provence-Alpes-Côte-d'Azur region) (Fig. 2). In France, the species appears to be extremely rare and localized. So far it has only been found at two sites separated by

less than 5 km; at each site, only few individuals were observed (the estimated number of individuals was 3 and 10–20, respectively). The search for the species was unsuccessful in several other localities in the French southern Alps with populations of *Onosma tricerosperma* subsp. *fastigiata*. These localities were situated 10 km to 18 km to the east, the north and the southwest of the two known sites of *H. onosmaevae*. Localities surveyed were the Bachelard valley above Fours-Saint-Laurent (Alpes-de-Haute-Provence, Uvernet-Fours, 44.32°N, 6.69°E) between 1750 m and 1900 m on 11.7.2019 and 27.6.2020, the Ubaye upper-valley, around la Barge and Maljasset (Alpes-de-Hautes-Provence, Saint-Paul-sur-Ubaye, 44.59°N, 6.83°E) between 1700 m and 2150 m on 11.7.2019 and 25.6.2020, the Ubayette valley, around Larche (Alpes-de-Haute-Provence, Larche, 44.45°N, 6.45°E) between 1650 m and 2000 m on 13.7.2019, above Saint-Ours (Alpes-de-Haute-Provence, Val d'Ornaye, 44.48°N, 6.81°E) between 1800 m and 1950 m on 26.6.2020, and the Barlatte upper-valley (Alpes-Maritimes, Châteauneuf-d'Entraunes, 44.18°N, 6.83°E) between 1700 m and 1850 m (MNP core area) on 25.6.2022. However, some of these unsuccessful visits were not performed under ideal conditions (e.g. end of blooming time or low abundance of blooming host plants), so that the occurrence of *H. onosmaevae* at all these sites cannot be excluded with certainty.

Field observations. Field observations were conducted at the “Vallon du torrent de Jalorgues” (Figs 15, 22) on 23.6.2020, when *Hoplitis onosmaevae* was found for the first time, and on 28.6.2020. The first visit took place in good weather conditions and lasted from 10:00 to 15:30. Several females and males were seen, most observations and pictures were realized on that day and a nesting site was found. During the second visit, fewer individuals were observed, possibly due to the less favorable weather conditions and we focused on a closed nest found five days before, around which a single female was seen.

Behaviour at *Onosma* stands. Several females were observed collecting pollen and nectar on flowers of *Onosma tricerosperma* subsp. *fastigiata* (Figs 18, 20, 21). After landing on the corolla, they entered the flower headfirst, clung to the style and then vibrated the flower by buzzing to extract the pollen. This behavior was observed several times. Each visited flower was sonicated usually twice during a few seconds. The females then collected nectar on the same flower and repeated the same sequence on the next flower. The bees landed frequently on the ground or on a stone between two flower visits to concentrate the nectar by widely spreading the mandibles and the labrum and slightly unfolding the proboscis (Fig. 19). Males were observed patrolling *Onosma* patches in their search for females, resting frequently nearby on the ground or on a stone (Figs 16, 17). They sometimes interrupted their patrolling flights to ingest nectar from *Onosma* flowers.

Pollen hosts. The pollen contained in the female scopae and the brood cells was morphologically identical to reference pollen samples of *Onosma*; while the French

samples certainly belong to *Onosma*, the unambiguous identification of *Onosma* pollen was not possible for the Turkish samples, as several closely related Boraginaceae genera with similar pollen morphology occur in Turkey.

Nesting biology. A nesting site was found on 23.6.2020 in the “Vallon du torrent de Jalorgues” by observing the flight direction of a female leaving the main patch of host plants. The nesting site was situated at a distance of approximately 35–40 m from the *Onosma* patch, where three dead trunks of larch (*Larix decidua* Miller, 1768) were present, one lying and two still standing (Fig. 22). Two nests in preexisting insect burrows were discovered, one in the lying trunk and the other in a standing trunk. One nest was left untouched, while the second was partially opened five days later. This nest consisted of an unknown number of brood cells, of which the two outermost were excavated. These cells were in line and parallel to the external surface of the tree trunk. The following nest architecture was observed (Fig. 25): 1. a nest plug composed of small pebbles glued together with fine sand, which was probably mixed with secretions (Fig. 23); 2. an empty chamber; 3. a partition constructed with sand, but without pebbles; 4. the outermost cell containing a solid provision mass (egg or larva not visible); 5. a partition built with sand; 6. the penultimate cell containing a solid provision mass (egg or larva not visible); 7. another partition built with sand.

Discussion

Biogeography

In the past twelve years, numerous new bee species have been discovered in mainland France. These new discoveries mainly concern species known from adjacent or other European countries (Vereecken and Barbier 2009; Aubert et al. 2010; Dufrêne et al. 2014; Aubert 2016; Genoud and Dufrêne 2016; Gabiot and Dufrêne 2018; Le Divelec 2020; Le Divelec and Aubert 2020). Alternatively, some of the newly discovered taxa are cryptic species that were previously confused with closely related taxa (Ghisbain et al. 2018; Praz et al. 2019, 2022; Kasparek 2020; Litman et al. 2021). The discovery of overlooked, newly immigrated or cryptic species may continue or even accelerate in the future as interest in bees increases and identifications and species delimitation are more and more complemented by DNA analyses. Much rarer, however, is the discovery of morphologically well characterized bee species that are new to science, such as *H. onosmaevae*.

This discovery is particularly remarkable as this species shows a highly disjunct distribution, occurring in southern France and at least 2000 km away in Turkey and Iraq. The morphology of both females and males of the European and the Asian populations is completely identical including the shape of the male antenna and the form of the membranous appendage of male sternum 6, which are highly diagnostic characters in the subgenus *Hoplitis*.

Thus, these disjunct populations are treated here as conspecific despite the lack of genetic data for the eastern populations. The bumblebee *Bombus brodmannicus* Vogt, 1909 shows an even more disjunct distribution occurring in the southern Alps and the eastern Pontic Mountains, the Armenian highlands and the Caucasus (Rasmont and Iserbyt 2014). Another putative *Onosma* specialist was discovered in France just a few years ago, *Eucera breviceps* (Friese, 1911), which was previously known only from Turkey and Syria (Aubert et al. 2024). It recently turned out, however, that this species is also present in Greece, Bulgaria and Italy. It cannot be excluded that *H. onosmaevae* also occurs in mountainous areas between France and Turkey, e.g. in Italy or the Balkans, where the bee fauna has not yet been thoroughly studied. In fact, the occurrence of *H. onosmaevae* in Bolu province close to the European part of Turkey renders the new species' occurrence in Greek mountain ranges quite probable.

Host plants

Hoplitis species of the subgenus *Hoplitis* show a tight association with two plant families, the Boraginaceae and the Fabaceae (Sedivy et al. 2013a). Although our results are based on few samples only, analyses of pollen contained in the female scopae and the brood cells as well as field observations strongly suggest that *H. onosmaevae* sp. nov. is narrowly oligoleptic on *Onosma*. The long mouthparts and the ability to buzz the flowers are clearly adaptations for the collection of nectar and pollen from *Onosma*. Pollen collection on Boraginaceae genera with narrow-tubed flowers requires morphological or behavioral adaptations known to occur in numerous species of diverse bee groups including *Hoplitis* species of the subgenus *Hoplitis* (Müller 1995). Among the *Hoplitis* species of the *adunca* group, *H. flabellifera* (Morice, 1901) possesses curved bristles on the front tarsi used to extract pollen from flowers of the genus *Anchusa* L. (Sedivy et al. 2013a). The recently discovered *H. lithodora* Müller, 2012 has specialized hooked bristles on the galeae of the proboscis, which serve to scratch pollen out of the narrow corolla of the flowers of *Lithodora*, its exclusive pollen host (Müller 2012; Aubert 2016). Among the *Hoplitis* species of the *annulata* group, *H. aqabaensis* (Warncke, 1991), oligoleptic on *Echiochilon* Desfontaine, has long and stiff pollen-collecting bristles on the ventral side of the first segment of the labial palpi and the base of the second segment (Sedivy et al. 2013a). In the *persica* species group, *Hoplitis persica* (Warncke, 1991), which is presumably oligoleptic on *Heliotropium*, has apically curved and capitate bristles on the second segment of the labial palpi most probably used to extract pollen from the narrow-tubed *Heliotropium* flowers (Sedivy et al. 2013a).

In contrast to the Boraginaceae genera mentioned above, pollen collection on flowers of *Onosma* does not require morphological specializations on proboscis or front legs.

In this genus, the pollen is shed into a cone that is formed by the five adjacent anthers and can be extracted either by buzzing or with mandibles and fore legs (Teppner 1995, 2011; Trunz et al. 2020). Beside *H. onosmaevae*, four additional species of the subgenus *Hoplitis* are known to apply buzzing to extract pollen from cone-shaped flowers of the Boraginaceae (Sedivy et al. 2013a): *Hoplitis holmboei*, which is oligoleptic on several genera of the Boraginaceae, such as *Onosma*, *Echium* and *Lithodora*, *H. homalocera*, which exclusively collects pollen on *Podonosma* Boiss., a close relative of *Onosma*, and two undescribed species of *Hoplitis* (*Hoplitis* sp. nov. 2 and *H. sp. nov. 3* in Sedivy et al. 2013a), which buzz the flowers of *Onosma* and *Trichodesma* R. Brown, respectively. At least two species that belong to other families than Megachilidae are also known to buzz the flowers of *Onosma*: *Eucera breviceps*, oligoleptic on *Onosma* (Aubert et al. 2024), and the short-tongued bee *Andrena symphyti* Schmiedeknecht, 1883, oligoleptic on Boraginaceae and known to collect pollen also on *Symphytum* L. and *Cerinthe* L. (Teppner 2011). The females of *Osmia apicata* Smith, 1853, a Boraginaceae oligolege with a strong preference for *Onosma* (Haider et al. 2013), do not buzz the *Onosma* flowers but scrape the pollen out of the cone with their fore legs after intruding their head into the corolla (Gogala and Surina 2011). The front legs of *H. onosmaevae* are probably not involved in pollen collection, although the females insert the head and the front part of the mesosoma into the corolla. Instead, by placing the ventral side of the mesosoma against the style (Fig. 20), the vibration of the thorax is transmitted to the cone through the style during buzzing (Buchmann 1983; Teppner 2018). The extraordinarily elongated proboscis of *H. onosmaevae*, which is probably not used for pollen extraction, allows males and females to access the nectar, which accumulates at the base of the *Onosma* corolla tube.

The phylogenetic position of *H. onosmaevae* strongly suggests that specialization on *Onosma* has occurred at least twice among species of the *adunca* group, once in *H. onosmaevae* and once in the clade containing *H. holmboei* and *Hoplitis* sp. nov. 2, whereas *H. holmboei*, and possibly *Hoplitis* sp. nov. 2, also collect pollen from other genera of Boraginaceae. The phylogenetic position of *H. linguaria*, which is most probably oligoleptic on *Onosma* (Müller 2023b), and of *H. semilinguaria*, which might also be an *Onosma* oligolege due to its long proboscis, is unknown. However, morphology suggests that they are not closely related to *H. onosmaevae*, which differs from these two species by the presence of a marginal rim and a medioapical spine on S6, two characters that *H. onosmaevae* shares with its closest relatives *H. adunca*, *H. benoisti* and *H. manicata*. Whether *H. linguaria* and *H. semilinguaria* are closely related to each other or to *H. holmboei* will require further investigation; depending on their phylogenetic position, specialization on *Onosma* may have independently evolved two, three or even four times in the subgenus *Hoplitis*.

Nesting biology

The nesting biology is unknown for more than two thirds of the *Hoplitis* species of the *adunca* group (Müller 2023b). Most species for which the nesting habits are known build their nests exposed in depressions of rocks or hidden within rock cavities and all use sand as nesting material, often combined with small pebbles (Sedivy et al. 2013b). Exceptions are *H. fertoni* (Pérez, 1890), which uses snail shells as nesting site, as well as *H. adunca* and *H. manicata*, which nest in insect burrows in dead wood and hollow stems beside other types of preexisting cavities. Interestingly, *Hoplitis onosmaevae*, which is closely related to the latter two species based on our phylogenetic analysis, was found to build its nests also in insect burrows in dead wood, suggesting that nesting in existing cavities in wood or stems has probably evolved only once in the subgenus *Hoplitis*. Whether *Hoplitis benoisti*, which builds its nests in depressions and cavities in rocks or in insect burrows in the soil (Sedivy et al. 2013b), has reverted to the ancestral nesting behaviour of the *adunca* group or whether it is sister to the other three species suggesting the origin of nesting in wood and stems in the ancestor of *H. adunca*, *H. manicata* and *H. onosmaevae* is unclear, since the phylogenetic relationships of these four species are not resolved.

Conservation

The extreme rarity of *Hoplitis onosmaevae* in France, where it is currently known only from two restricted and little distant localities, does not seem to be fully accounted for by the rarity of its host plant, since large *Onosma tricerosperma* subsp. *fastigiata* populations are known outside the known range of *H. onosmaevae*, for example in the southern part of the Massif Central and at lower altitudes in the southern Alps. *Hoplitis onosmaevae* was only found at elevations between 1900 m and 2000 m in France and between 1075 m and 2350 m in Turkey and Iraq. This suggests that *H. onosmaevae* may have a particularly narrow climatic niche in France and does not find suitable climatic conditions at lower elevations, despite the presence of the host plant. This situation is reminiscent of that of *Bombus brodmannicus*, which is also much more narrowly distributed in the Alps than its host plant, *Cerinthe* (Boraginaceae). Possibly, these two bee species are associated with climatic conditions that are only found at certain elevations in restricted areas of the southern Alps, for example humid and cold winters and particularly hot and dry summers. Other factors may also limit the distribution of *H. onosmaevae*, particularly the presence of dead wood as nesting substrate, which represents a scarce resource in the steppe-like grasslands, where *Onosma* plants preferentially grow. The local history of forest use by humans may also partly explain the rarity of *H. onosmaevae*; massive deforestation in the

southern Alps from approximately 2000 BC (Beaulieu 1977) may have reduced the area of habitat suitable for the species by reducing the number of its potential nidi-fication sites.

The strongly disjunct distribution of *H. onosmaevae* and the bee's extremely local occurrence in limited areas of the southern French Alps have important implications for conservation. The species has most probably a very narrow ecological niche, making it highly susceptible to future changes in its habitats, for example due to changes in agricultural practices or to climate change. Even if the two known sites of *H. onosmaevae* are located in the core area of the Mercantour National Park, human activities can threaten its populations. Pastoralism, for example, is a significant economic activity in the Park and considered as an important heritage, playing a role in maintaining open habitats (Parcs nationaux de France 2012). However, excessive pastoral pressure or overgrazing can easily impact the populations of the host plants, either by direct consumption of the plants or by repeated trampling. The negative impact of excessive grazing could even be aggravated by unfavorable climatic conditions, such as prolonged droughts, which are expected to reduce the availability of flowers and further increase pressure on the vegetation. The presence of dead wood in close neighbourhood to the *Onosma* stands is a further essential prerequisite for the occurrence of *H. onosmaevae*, rendering the preservation and promotion of a sufficient supply of dead wood at the French sites occupied by *H. onosmaevae* essential.

Conclusions

Given the extreme rarity of *Hoplitis onosmaevae* in France and the species' high vulnerability to habitat changes due to its strong dependence on *Onosma* and dead wood, a detailed conservation plan should be worked out in the southwestern Alps, including the following measures: 1. additional fieldwork to identify further populations and to determine the current distribution of *H. onosmaevae*, including in the Italian Alps, where the species could also be present; 2. the active conservation of the known populations of *H. onosmaevae*, for example by adopting an appropriate management plan, ensuring that the habitat characteristics do not change and providing an adequate supply of plant and nesting resources for the bee, with the aim of increasing the overall size of the population; 3. adaptation of the eco-pastoral management plans in the regions of the Mercantour National Park where the species occurs, to preserve and increase the abundance of the *Onosma* stands.

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Supplementary material 1

Database for all specimens examined in this study

Authors: Matthieu Aubert, Andreas Müller, Christophe Praz
Data type: xlsx

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